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BRIEFER ARTICLES

THE MICROSPOROPHYLLS OF GINKGO

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 134

(WITH PLATE VII)

This study was undertaken in the first place to determine the origin of the mucilage ducts in the hump of the microsporophyll. As there is a general resemblance among the microsporophylls of Taxus, Torreya, and Ginkgo, and as in Torreya, according to COULTER and LAND[1] (p. 163), the resin ducts are formed from the disorganization of three of the seven sporangia, it seemed possible that in Ginkgo the mucilage ducts might have been formed from abortive sporangia also. As my material showed the development of the strobili and microsporangia, I have included an account of them, so as to give a general history of the development of the microsporophyll. The buds were collected during July, August, and September of 1907 from a tree in Elyria, Ohio, in grounds then owned by Mr. I. W. METCALF. Thanks are due him for the material and also Professor F. O. GROVER of Oberlin College and Mr. FRED STOKEY for collecting.

Development of the strobili

The strobili which will mature pollen the following year are formed in June or early July, but are hidden in buds which cannot be distinguished from leaf buds. In the latter part of July, if the scale leaves are removed from the buds, the strobili can be seen as small papillae in the axils of the scale leaves. Examined with a microscope, strobili of the same bud often show different stages of development, some being short, with the sporophylls just evident as small rounded elevations (*fig. 1*), others being elongated cones with the lower sporophylls beginning to show differentiation into sporogenous part and hump (*fig. 2*). The development of the two sides of the strobilus is often very uneven, due to greater crowding on one side than on the other. At this stage there is no differentiation of tissue in the sporophylls at the top of the strobilus, but in those lower down mucilage ducts are beginning to form in the most external portion of the sporophylls; and in sporophylls at the base the ducts are fully formed and functioning sporogenous tissue is beginning to be evident in the part nearest the axis. Occasionally the sporangium that will finally function appears in advance of the mucilage ducts, or the two may start together, but generally the ducts are formed before the functioning sporogenous tissue is very evident. By August 8 the sporophylls at the base of the strobilus show the formation of the stalk and the elongation of the functioning sporangium (*fig. 3*), while the sporophylls from the base to half-way up the strobilus have well-developed mucilage ducts. The stalks are formed by an increase in the number of cells as well as by elongation of the cells. By August 20 all the sporophylls have stalks and mucilage ducts, but the functioning sporogenous tissue is conspicuous only in the lower sporophylls. Early in September (*fig. 4*) the strobili have reached a length of 3^{mm}, the sporophylls have the typical shape, the mucilage ducts are enormous, and the cells of the sporogenous mass are separating for the mother cell stage, which the oldest sporangia reach before winter, according to SPRECHER[2] (p. 156). Material that I collected in April shows some sporangia in the mother cell stage and others with tetrads formed.

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[1] COULTER, JOHN M., AND LAND, W. J. G., Gametophytes and embryo of *Torreya taxifolia*. BOT. GAZETTE 39:161–178. *pls. A, 1–3.* 1905.

Development of the functioning sporangium

The early development of the functioning sporangium is probably like that of the cycads,[3] though I have not yet been able to determine that the archesporium starts as a single cell, but stages like that in *fig. 5* probably indicate that a single cell has divided anticlinally and then periclinally. Sometimes the order seems to be reversed. The outer cells are the primary wall cells, giving rise to several layers of wall cells with scanty cytoplasm; the inner are the primary sporogenous cells, by further division producing a large mass of sporogenous cells with dense cytoplasm, larger nuclei with heavily staining chromatin, and frequently conspicuous nucleoli. In the mature sporangium the hypodermal layer of cells and the layer below it have thickening bands in the walls, and in the upper part of the sporangium near the mucilage duct the walls of deeper cells are also thickened. In this respect the microsporangium of Ginkgo differs from the microsporangium of all other gymnosperms and is like that of angiosperms.

The tapetum seems to come entirely from the sporogenous mass.

Development of the mucilage ducts

The upper, sterile part of the sporophyll is developed into a humplike projection called by ČELAKOVSKÝ[4] (p. 283) a crest (*crista*). In this are large mucilage ducts, cells containing calcium oxalate, and epidermal cells containing tannin. The mucilage ducts begin development like sporangia, and for some time look like the functioning sporogenous tissue in the lower part of the sporophyll. Several hypodermal cells are differentiated from the rest by their greater size and their more vacuolate contents (*fig. 6*). Each of the cells divides into an outer and an inner cell, suggesting the primary wall cell and primary sporogenous cell of the cycads (*fig. 7*). The inner cells by further division produce a mass of deeply staining tissue beneath several layers of cells with scanty cytoplasm formed by the division of the outer cells (*fig. 8*). As soon as this stage is reached the walls of the central mass of cells begin to disintegrate, probably by becoming mucilaginous (*fig. 9*), as soon the nuclei appear to be floating in a cavity filled with mucilage. Then the nuclei also disintegrate, and some of them with the remains of their surrounding cytoplasm are flattened against the wall of the widening cavity, forming a tapetum-like layer (*fig. 10*). Finally the whole central mass is replaced by a mucilage cavity.

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[2] SPRECHER, ANDREAS, Le *Ginkgo biloba* L. pp. 206. *figs. 225*. Genève. 1907.

[3] SMITH, FRANCES GRACE, Morphology of the trunk and development of the microsporangium of cycads. BOT. GAZETTE 43:187–204. *pl. 10*. 1907.

[4] ČELAKOVSKÝ, L. J., Die Vermehrung der Sporangium von *Ginkgo biloba* L. Oesterr. Bot. Zeitschrift 50:276–283. 1900.

Discussion of the nature of the hump

The sporophylls of Ginkgo resemble those of Taxus and Torreya. Taxus has a group of sporangia, five or more in number, surrounding a central axis. Torreya has four sporangia on one side of the axis, but in the primary sporogenous cell stage seven sporangia appear; three of these disorganize, being replaced by a single large resin cavity, leaving only four to come to maturity. Ginkgo has two sporophylls on one side of the axis, surmounted by the conspicuous hump containing mucilage ducts. The development of the mucilage ducts from what appear to be abortive sporangia seems to indicate that the microsporophylls of Ginkgo may have come from a peltate type like that of Taxus. The fact that the sporophylls of living Ginkgo sometimes, and of fossil Ginkgoales as Baiera regularly, bear more than two microsporangia is additional evidence in favor of this view.

The case would be quite clear if evidence could stop with the hump, but in examining the mucilage ducts in the leaves, I find that they also at first look like sporogenous tissue (*fig. 11*). So there are three lines of development that resemble one another: the functioning sporogenous tissue, the mucilage ducts in the hump of the sporophyll, and the mucilage ducts in the leaves; all have the same early history, starting with one or more cells which divide periclinally into outer and inner cells, the inner by further division forming a deeply staining mass, the outer forming several layers of wall cells. The tissue formed in the functioning sporangium we know is sporogenous as it later produces spores; the tissue in the hump of the sporophyll that forms mucilage ducts, we think is sporogenous from analogy with Torreya and Taxus; but as to the mucilage ducts in the leaves we have no evidence that the tissue is sporogenous. Can we say that the ducts in the leaves, though they look like abortive sporangia, are not abortive sporangia, while the ducts in the hump having the same appearance are really abortive sporangia? On the other hand, does the presumption that the ducts in the leaves are not abortive sporangia forbid entirely the view that the ducts in the hump are abortive sporangia?

It seems reasonable to conclude, if the resin cavity of Torreya originates in abortive sporangia, that the mucilage ducts of Ginkgo also owe their origin to abortive sporangia.

Summary

1. The development of the strobilus proceeds from the bottom toward the top, the oldest sporophylls being at the base.
2. The development of the functioning microsporangium is probably like that of the cycads.
3. The development of the mucilage ducts in the hump of the microsporophylls is in general like that of sporogenous tissue.
4. This origin of the mucilage ducts in the hump may indicate that the microsporophylls of Ginkgo have come from a peltate type like the microsporophylls of Taxus.

I wish to acknowledge my indebtedness to Professor CHARLES J. CHAMBERLAIN, by whose suggestion and under whose direction the work was done.—ANNA M. STARR, *The University of Chicago.*

EXPLANATION OF PLATE VII

FIG. 1.—Longitudinal section of young strobilus, with sporophylls beginning to be evident; August 7. ×20.

FIG. 2.—Longitudinal section of older strobilus, with mucilage ducts (*d*) and sporogenous tissue (*s*) starting at the base; July 29. ×20.

FIG. 3.—Longitudinal section of strobilus older than *fig. 2*, showing development proceeding toward the top; August 7. ×20.

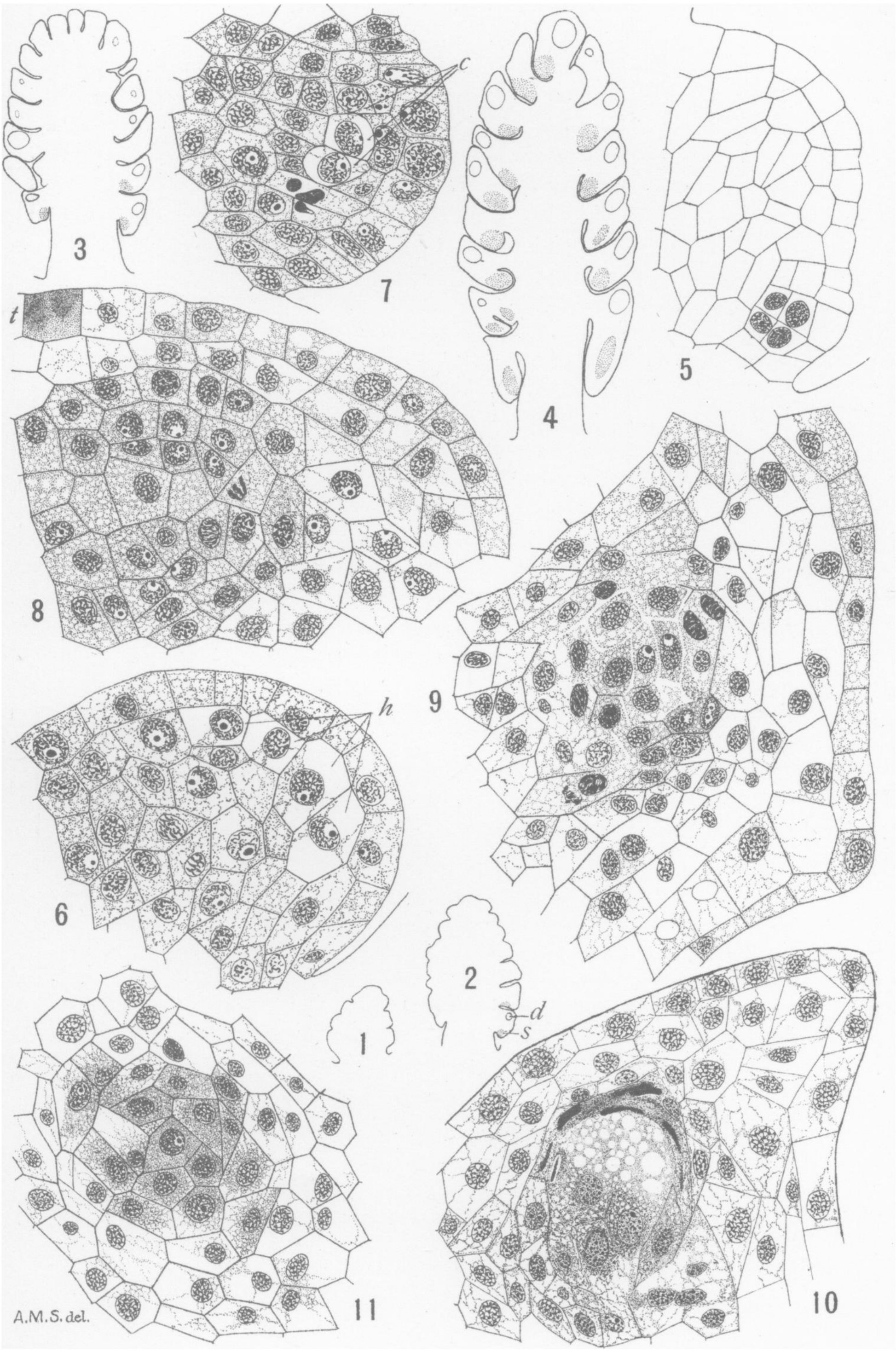
FIG. 4.—Longitudinal section of strobilus with mucilage ducts in all the sporophylls and the sporangia in the mother cell stage; September 2. ×20.

FIG. 5.—Longitudinal section of young sporophyll, showing four cells that have probably come from a single archesporial cell. ×485.

FIG. 6.—Longitudinal section of the hump of a young sporophyll showing a hypodermal plate of four cells (*h*) strongly differentiated. ×485.

FIG. 7.—Longitudinal section of the same region of another sporophyll with three hypodermal cells (*c*) that have divided periclinally. ×485.

FIG. 8.—Longitudinal section of the same region of an older sporophyll



STARR on GINKGO

showing differentiation into wall cells and a central mass of cells like sporogenous tissue. ×485.

Fig. 9.—The walls of the cells of the central mass are becoming mucilaginous and some of the nuclei are disintegrating. ×485.

Fig. 10.—The mucilage cavity is formed, some nuclei still floating in the fluid contents, others being flattened against the wall. ×485.

Fig. 11.—Section of an early stage of a mucilage duct in a leaf, showing cells resembling sporogenous tissue. ×485.

ALTERNATION OF GENERATIONS AND SEXUALITY IN *DICTYOTA DICHOTOMA*

After the failure of many attempts made during the past three summers to raise *Dictyota dichotoma* (Huds.) Lamour. from the spores and fertilized eggs to maturity, I have succeeded in raising nearly 100 plants to a fruiting condition. Since all attempts to raise plants to maturity in the laboratory have failed so far, the cultures were started in the laboratory and then transferred to the harbor. The method employed was as follows. Several days before the time for the maturing of the crop of sexual cells, when therefore no eggs were present in the water to serve as a possible source of contamination, two good fruiting tetrasporic plants were gathered late in the afternoon and placed in two jars of sea water, one in each jar. Since the spores will not attach themselves to glass, oyster shells which had lain on land for several years were placed in these jars. On the following day many tetraspores had been liberated and had attached themselves to the shells. The parent tetrasporic plants were then removed.

On the day when eggs and spermatozoids were mature, several sexual plants were gathered late in the afternoon and placed in a jar of sea water with oyster shells in the bottom, as before. Abundant liberation of eggs and spermatozoids occurred the next morning, as usual, and the parent sexual plants were then removed.

Three cultures were thus obtained, one containing fertilized eggs, and the other two containing tetraspores, each of the latter containing the spores from a single plant. These cultures were placed in front of a north window of the laboratory.

After about two weeks, when the young plants had reached a height of $1.5-2^{mm}$,[5] one shell bearing many young plants was removed from each of these jars and suspended between posts about 30^{cm} below low water in a favorable situation in the harbor, and all plants of Dictyota in the immediate vicinity were removed.

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[5] This rate of growth is probably less than normal, since plants of Dictyota grow much more slowly in cultures than they do under natural conditions.